A NEW SPECIES OF *BRYANTOLEPIS* CAMP, WELLES, AND GREEN, 1949 (PLACODERMI, ARTHRODIRA) FROM THE EARLY DEVONIAN WATER CANYON FORMATION OF NORTHERN UTAH AND SOUTHERN IDAHO, WITH COMMENTS ON THE ENDOCRANIUM

DAVID K. ELLIOTT

Department of Geology
Northern Arizona University, Flagstaff, Arizona 86011-4099
David.Elliott@nau.edu

AND **ROBERT K. CARR**

Department of Biological Sciences
Ohio University, Athens, Ohio 45701

ABSTRACT

A new species of the actinolepidoid arthrodire *Bryantolepis* Camp, Welles, and Green, 1949, is described from the Water Canyon Formation of northern Utah and southern Idaho, where it is characteristic of the uppermost part of the Lower Devonian in the Grassy Flat Member. *Bryantolepis williamsi* n. sp. is about 60% larger than the only other previously recognized species, *B. brachycephala* (Bryant, 1932), from the Early Devonian Beartooth Butte Formation of Wyoming, but is otherwise very similar to it. The new material provides information on the endocranial morphology showing that it is very similar to that of *Kujdanowiaspis* Stensiö, 1942 and *Lehmanosteus* Goujet, 1984, the only other actinolepidoids for which the endocranium is known. The parasphenoid is described for the first time in this genus, as is the anterior superognathal. The superognathal is only the second to be definitely attributed to an actinolepidoid and is shown to be a crushing rather than a shearing element.

Introduction

Placoderms are early, jawed fishes that are almost exclusively Devonian in age. Within the Placodermi M'Coy, 1848, the major group is the Arthrodira Woodward, 1891, the most basal members of which are the Actinolepidoidei Miles, 1973 (now thought to be a paraphyletic group [Dupret, 2004; Dupret et al., 2009; Figure 1]). Five genera and six species of actinolepidoids have been described previously from the Beartooth Butte and Water Canyon Formations and the Sevy Dolomite of the western United States (Bryant, 1932, 1934, 1935; Denison, 1958; Johnson et al., 2000), and in this paper an additional species of the actinolepidoid *Bryantolepis* Camp, Welles, and Green, 1949, *Bryantolepis williamsi* n. sp., is described from the Water Canyon Formation of northern Utah and southern Idaho. As the genus had previously only been known from the Beartooth Butte Formation of Wyoming the new species extends the range of the genus and supports the correlation between the Beartooth Butte Formation and the Grassy Flat Member of the Water Canyon Formation that had previously been proposed (Elliott and Johnson, 1997).

Despite their age, the morphology of placoderms is known in considerable detail. This is particularly true of the cranial anatomy, which was minutely studied by Stensiö who used serial-grinding techniques to determine the shape of the cranial cavities and the position of canals and foramina for nerves and vessels (Stensiö, 1963a, b; Stensiö, 1969). Serial grinding provides remarkable detail but it is destructive of the specimen and also extremely time consuming so it was not until the advent of preparation using acetic acid that additional information started to be obtained from well-preserved arthrodire endocrania. More recent studies by Young (1979, 1981), Goujet (1984), and Dupret (2010) have provided additional information on arthrodire cranial morphology, particularly on the structures surrounding the orbit (Young, 1979). However, the only actinolepidoids for which detailed information is available remain *Kujdanowiaspis* Stensiö, 1942, described in detail by Stensiö (1963b, with an update by Dupret, 2010), and *Lehmanosteus* Goujet, 1984. Thus the presence of a well-preserved endocranium in one specimen of *Bryantolepis williamsi* n. sp. helps to improve knowledge of variation in the cranial anatomy of this group of early, jawed fishes.

Geological Setting

The material described here was collected from the lower part of the Grassy Flat Member of the Water Canyon Formation at
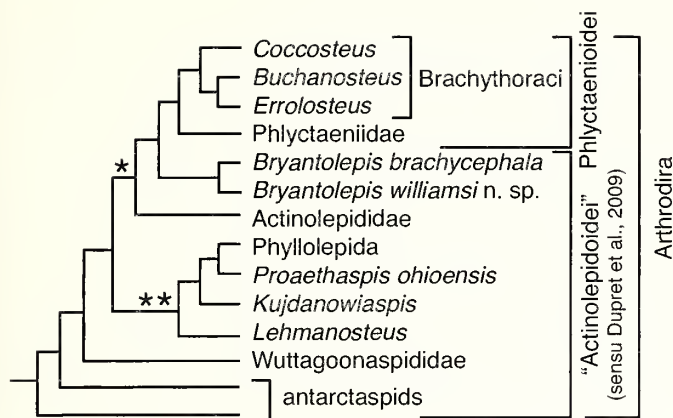
Figure 1. Hypothesis of relationships for arthrodiran taxa used in the text. Based on strict concensus tree of Dupret et al., 2009, fig. 3, with the addition of *Errolosteus* and *Bryantolepis williamsi* n. sp. *, **, nodes 20 and 8, respectively, of the Dupret et al. tree.

Green Canyon, east of Logan, northern Utah, and near St. Charles Creek, southern Idaho. Although only a few specimens are known, this species appears to be characteristic of the uppermost part of the Lower Devonian portion of the section. The Water Canyon Formation of northern Utah and southeastern Idaho consists of dolomites, dolomicrites, and dolomicritic quartz-arenites deposited within a restricted coastal embayment along the northwest coast of Euramerica (the Old Red Sandstone continent). It lies above the Silurian (Ludlovian–earliest Pridolian) Laketown Dolomite, which consists of mottled, dark grey to black, fossiliferous dolostone, and forms prominent cliffs in the study area.

The Water Canyon Formation is divided into the lower Card Member and the upper Grassy Flat Member (Williams and Taylor, 1964). The Card Member is unfossiliferous and is characterized by mottled, grey, thick- to very thick-bedded, dolomicrite at the base to light blue-grey, thinly bedded dolomicrite in the upper part. Near the top of the Card Member, the argillaceous content increases until the dolomite becomes arenaceous. The first occurrence of sand in the formation defines the base of the Grassy Flat Member (Williams and Taylor, 1964).

The lithologically more varied Grassy Flat Member is characterized by very thin- to medium-bedded laminated dolomicrite, laminated to massive argillaceous and arenaceous dolomicrite, and massive to planar trough cross-bedded dolomicritic and dolomitic quartz-arenite. The upper part of the member is more arenaceous and is capped by an intraformational breccia that forms prominent rounded cliffs at the top of the section, above which the Hyrum Dolomite occurs. Vertebrates occur throughout the lower part of the Grassy Flat Member but are largely limited to the argillaceous and arenaceous dolomicrite and dolomitic quartz-arenites (Reed, 1997). The new species of *Bryantolepis* described here occurs just below the more arenaceous upper part of the Grassy Flat Member in thick- to very thick-bedded silty dolostones. It occurs with *Allocryptaspis utahensis* Denison, 1953, and acanthodian spines in Green Canyon, but in St. Charles Creek it is associated with an extensive but undescribed fauna including a species of *Cardipeltis*

Branson and Mehl, 1931, at least two species of pteraspid, another arthrodire, and a species of *Uranolophus* Denison, 1968.

The Water Canyon Formation was deposited within a restricted coastal embayment along the northwest coast of the Old Red Sandstone continent. Restrictive conditions are thought to be the result of paleogeographic features such as the orientation of the basin, the position of the Tooele Arch, which flanked the southern margin of the basin, and the probable existence of a barrier along the basin's oceanward margin. The Card Member represents hypersaline, peritidal deposition and includes mainly subtidal to intertidal lithologies, although some supratidal lithologies are recognized. The Grassy Flat Member records fluvial influences and hyposaline conditions such as prodelta, delta, marginal delta basin, distributary channel, and estuarine sediments many of which record tidal influences (Reed, 1997).

Due to the lack of age-diagnostic invertebrates the Water Canyon Formation has been assigned a variety of ages, from the Upper Silurian to the Middle Devonian, since its initial description (Williams and Taylor, 1964; Johnson and Sandberg, 1977; Johnson et al., 1988; Elliott and Ilyes, 1996; Elliott and Johnson, 1997; Elliott et al., 2000). Temporal control was placed on the formation by Elliott and Johnson (1997), who correlated the vertebrate fauna at the base of the Grassy Flat Member to the basal Lippincot Member of the Lost Burro Formation of Death Valley, California, the Sandy Member of the Sevy Dolomite in east-central Nevada (Davis, 1983), and the Beartooth Butte Formation of Beartooth Butte in northern Wyoming (Dehler, 1995). The Beartooth Butte Formation has a spore determination of middle to late Emsian (Tanner, 1983) and thus provides the basis for an Emsian date for the lower part of the Grassy Flat Member. Reed (1997) has confirmed this age by the correlation of transgressive-regressive cycles through the Water Canyon Formation to those established for the Devonian of Euramerica by Johnson et al. (1985). In addition to placing more accurate temporal constraints on the formation as a whole the eustatic data suggests that the Card Member may be Pragian, although there is no supporting paleontological evidence, and that the upper part of the Grassy Flat Member is Eifelian to possibly earliest Givetian. The latter is supported by the presence of a species of *Asterolepis* Eichwald, 1840, osteolepids, *Holoptychius* Agassiz, 1839, and the pteraspid *Psephaspis williamsi* Ørvig, 1961, all of which are indicators of the Middle Devonian (Elliott and Johnson 1997; Elliott et al., 2000). The overlying Hyrum Dolomite provides an upper age constraint as it is dated to the early Givetian based on the presence of the *Stringocephalus* biozone near its base (Stokes, 1986; Johnson et al., 1988).

Materials and Methods

The material consists of disarticulated cranial and post-cranial material preserved in a silty dolostone. The specimens were prepared mechanically using a vibrotool with a tungsten-carbide bit. The specimens are deposited in the collections of the University of Kansas Museum of Natural History, and bear their catalog numbers (prefixed KUVP). Phylogenetic analyses were conducted using PAUP* (v.4.0b10, Swofford, 2002). Data was based on the published matrix of Dupret et al. (2009) with the addition of *Bryantolepis williamsi* n. sp. and new scoring for their characters 1–4. Characters were considered unordered with a heuristic search conducted using a random-addition sequence with ten repetitions (holding 100 trees).
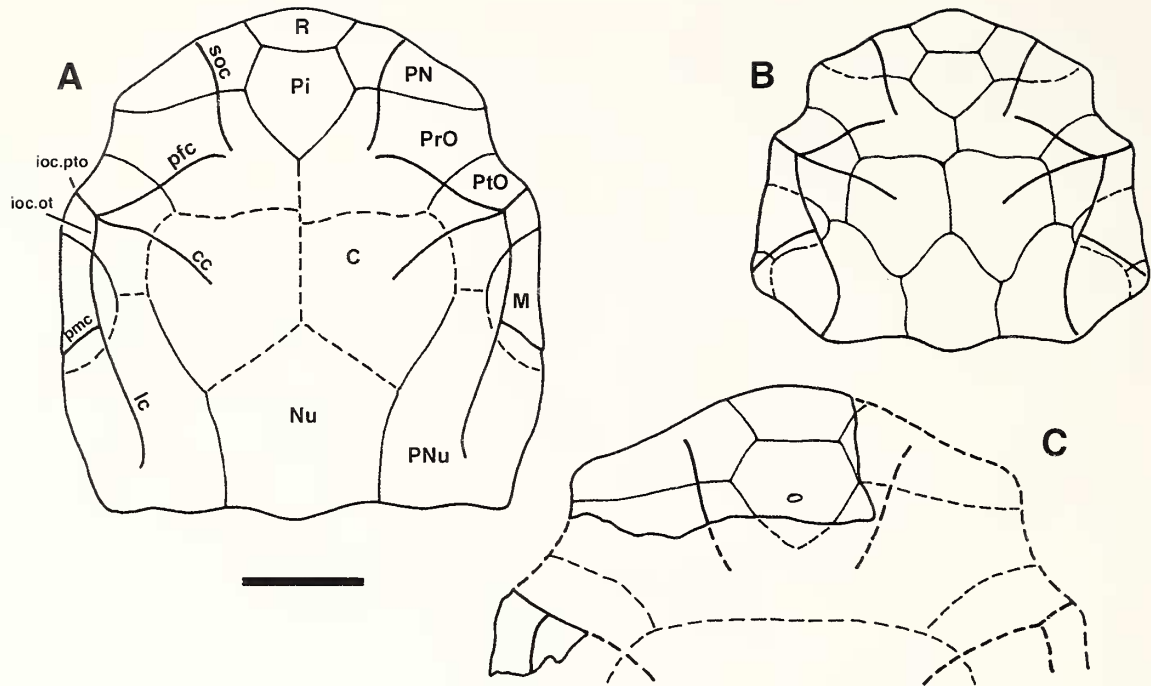
Figure 2. Reconstructions of the skulls of *Bryantolepis* species drawn to the same scale. A, *Bryantolepis williamsi* n. sp. B, *Bryantolepis brachicephala*. C, *Bryantolepis* sp. (B and C redrawn from Denison, 1958). Key: cc, central-canal groove; C, central plate; ioc.ot, otic branch of the infraorbital-canal groove; ioc.pto, postorbital branch of the infraorbital-canal groove; lc, lateral-canal groove; M, marginal plate; Nu, nuchal plate; PNu, paranuchal plate; pfc, profundus-canal groove; P, pineal plate; PN, postnasal plate; pmc, postmarginal-canal groove; PrO, preorbital plate; PtO, postorbital plate; R, rostral plate; soc, supraorbital-canal groove. Scale bar equals 1 cm.

Systematic Paleontology

Class PLACODERMI M'Coy, 1848
Order ARTHRODIRA Woodward, 1891
Suborder "ACTINOLEPIDOIDEI" Miles, 1973
UNNAMED FAMILY
Genus *BRYANTOLEPIS* Camp, Welles, and Green, 1949

Diagnosis

Preorbital plates wide, deeply notched anteriorly by a very large pentagonal pineal plate. Postnasal plates large and together with rostral and pineal plates fused to the rest of the cranial roof. Distinct profundus sensory-canal grooves extend from the preorbital to the postorbital plates.

Type species

Bryantolepis brachycephala (Bryant, 1932).

Remarks

Bryantolepis was originally named *Euryaspis* Bryant, 1932, and described from material from the Lower Devonian Beartooth Butte Formation at Beartooth Butte, Wyoming. *Bryantolepis brachycephala*, the type species (Figure 2B), was considered by Denison (1958, 1978) to be the only valid species, as *B. obscurus* Bryant, 1934, and *B. cristata* Bryant, 1934, are doubtfully distinct and are considered to be conspecific with *B. brachycephala*; and *B. major* Bryant, 1935, was based on a specimen that was considered to be cranial but is probably an imperfectly preserved median dorsal of *Anarthraspis* Bryant, 1934 (Denison, 1958). The only

other *Bryantolepis* specimen reported comes from the Water Canyon Formation at Green Canyon near Logan, Utah (Denison, 1958, p. 492–493; Figure 2C). This specimen is the poorly preserved anterior part of a skull roof showing the rostral, pineal, and postnasal plates, and parts of the preorbital and postorbital plates. The large five-sided pineal plate and the large and wide postnasal plate show that this is *Bryantolepis*, but it is considerably larger than the type species (Figure 2B) and so was attributed only to *Bryantolepis* sp. by Denison (1958).

Bryantolepis williamsi n. sp.
Figures 2A, 3–7, 9–10

Diagnosis

Large species of *Bryantolepis* in which the nuchal and paranuchal plates are longer than broad resulting in a cranial roof that is also longer than broad.

Remarks

The incomplete anterior part of a *Bryantolepis* skull roof also collected from Green Canyon and described as *Bryantolepis* sp. by Denison (1958) is close in size and proportions to the type skull described here. Although slightly larger, it is assumed that this specimen is also an example of *Bryantolepis williamsi* n. sp.

Etymology

Named after Michael E. Williams, in recognition of his important contributions to our understanding of early vertebrates.

Holotype

University of Kansas Natural History Museum No. KUVP 141304 is a complete skull roof (Figure 3).

Horizon

All specimens are from the lower part of the Grassy Flat Member of the Water Canyon Formation, Green Canyon, northern Utah, and St. Charles, southern Idaho.

Additional material

KUVP 141305, the rostral part of a skull roof (Figure 2) associated with the type specimen; KUVP 141307, a right suborbital plate (Figure 4); KUVP 141308, a skull roof preserving the endocranium (Figures 5–7, 9); KUVP 141306, a right anterior-lateral plate with attached anterior ventral, interolateral, and spinal plates (Figure 10).

Description

Skull roof

The skull is represented by one complete skull roof preserved in dorsal view and associated with the incomplete rostral area of a separate skull (Figures 2A, 3), and a skull with endocranium preserved in ventral view (Figures 5–7, 9). The skull roof is broad and rounded anteriorly and the two complete skull roofs are both 40 mm in length and 36 mm in width. The dermal plates of the skull roof can be identified in much of the type specimen (Figures 2A, 3A) although the central part of this skull roof is weathered, making it difficult to delineate the plate margins in that area.

The rostral part of the skull is fused to the rest of the cranial roof, as is characteristic of *Bryantolepis*. Slight etching of this area due to weathering in the type specimen and the associated fragment has picked out marginal bands around the rostral, pineal, and postnasal plates that presumably relate to slight differences in composition as the plates grew marginally (Figure 3A). This complex of plates is essentially as in *B. brachycephala* and the pineal plate shows the pentagonal shape that is characteristic of the genus, although it appears to be a little more elongated than in the type species. The post-pineal part of the skull is clearly more elongated than in the type species, however, with the nuchal and paranuchal plates being proportionally much more elongated (Figures 2A, 3A; contrast with Figure 2B).

As is characteristic of the genus, distinct profundus sensory-canal grooves (pfc) extend from the preorbital to the postorbital plates. Grooves for the supraorbital canals (soc) traverse the postnasal plate and terminate at the ossification center of the preorbital plates. Four sensory grooves radiate from the ossification center of the postorbital plates: profundus sensory canal (pfc), postorbital (ioc.pto) and otic (ioc.ot) branches of the infraorbital canals, and central canals (cc). The otic branches of the infraorbital canals terminate at the ossification center of the marginal plates. From this point, grooves for the postmarginal canals (pmc) extend to the skull roof margin. The lateral-line canals (lc) extend posteriorly and terminate within the paranuchal plates rather than transecting the posterior margin as in the type species (Figures 2A, B, 3B).

Suborbital plate

A single right suborbital plate, incomplete anteriorly and preserved with the internal face visible, is included within the material of the new species (Figure 4). It shows a slight notch in the dorsal margin near its anterior edge that represents the position of the infraorbital canal that runs from this point below the orbital notch on the external surface. A postocular crista (cr.po) is present. Posteriorly, there is a contact face for the postsuborbital plate (cf.PSO). The overall shape for the suborbital plate accords well with that of *B. brachycephala* (Denison, 1958, fig. 106C).

Parasphenoid

A partial parasphenoid showing the ventral surface is still attached to the endocranium on KUVP 141308 (Figures 5–7). As preserved it shows the left side and is irregularly ovate in outline and gently concave. The entire surface of the bone is covered with small closely packed tubercles. It would be expected that the buccohypophysial duct should perforate the center of the bone as in other described examples; however, although there is a depression near the posterior median margin it appears to be floored with tubercles, and damage to the midline of the bone has destroyed other possible sites for this feature. An attempted reconstruction of the endocranium and associated features, accomplished by mirror-imaging the left side, shows the parasphenoid to be ovate, wider than long and gently concave (Figure 7). No paired lateral indentations or grooves are present although this feature is reported in other parasphenoids (Dennis-Bryan, 1995). In comparison to other described parasphenoids this is a large bone in relation to the size of the skull.

Dennis-Bryan (1995) noted descriptions of the parasphenoid in 33 arthrodire genera but pointed out that the number of specimens is small with only one or two examples for each species. This paucity of information is particularly true for actinolepidoids with parasphenoids having been described from only two genera. Stensiö (1963b) described *Kujdanowiaspis* as having a parasphenoid whose ventral surface is entirely covered by tubercles and with a large undivided median buccohypophysial foramen. The parasphenoid outline is oblong and longer than wide with a median notch on each side; however, the outline is uncertain (indicated by Stensiö's use of a dashed line for the reconstructed margin, e.g., Stensiö, 1963b, fig. 10A). The parasphenoid of *Lehmanosteus hyperboreus* Goujet, 1984 (fig. 107), is similar to that of *Kujdanowiaspis* in that the ventral surface is covered by tubercles and has a single buccohypophysial foramen at its center. It is wider than long, however, and has a pentagonal outline. Dennis-Bryan (1995) concluded that parasphenoids are species specific and show no feature or character that is specific to a higher taxon. However, she also noted that "primitive" and "advanced" parasphenoid types had been recognized in the past (Gardiner and Miles, 1990). The "primitive" type is usually flat and without notches or grooves; the ventral surface is covered with tubercles and there is a large medial buccohypophysial foramen, which may be single or paired. The "advanced" type is thicker, with lateral notches and grooves and the buccohypophysial foramina reduced; tubercles are reduced or absent, and a well-developed median crest is developed.

This specimen adds a third actinolepidoid species to those for which the parasphenoid is known. It appears to be "primitive" in structure, despite the lack of a recognizable buccohypophysial foramen, but it provides no new characters that indicate taxonomic value beyond the species level.
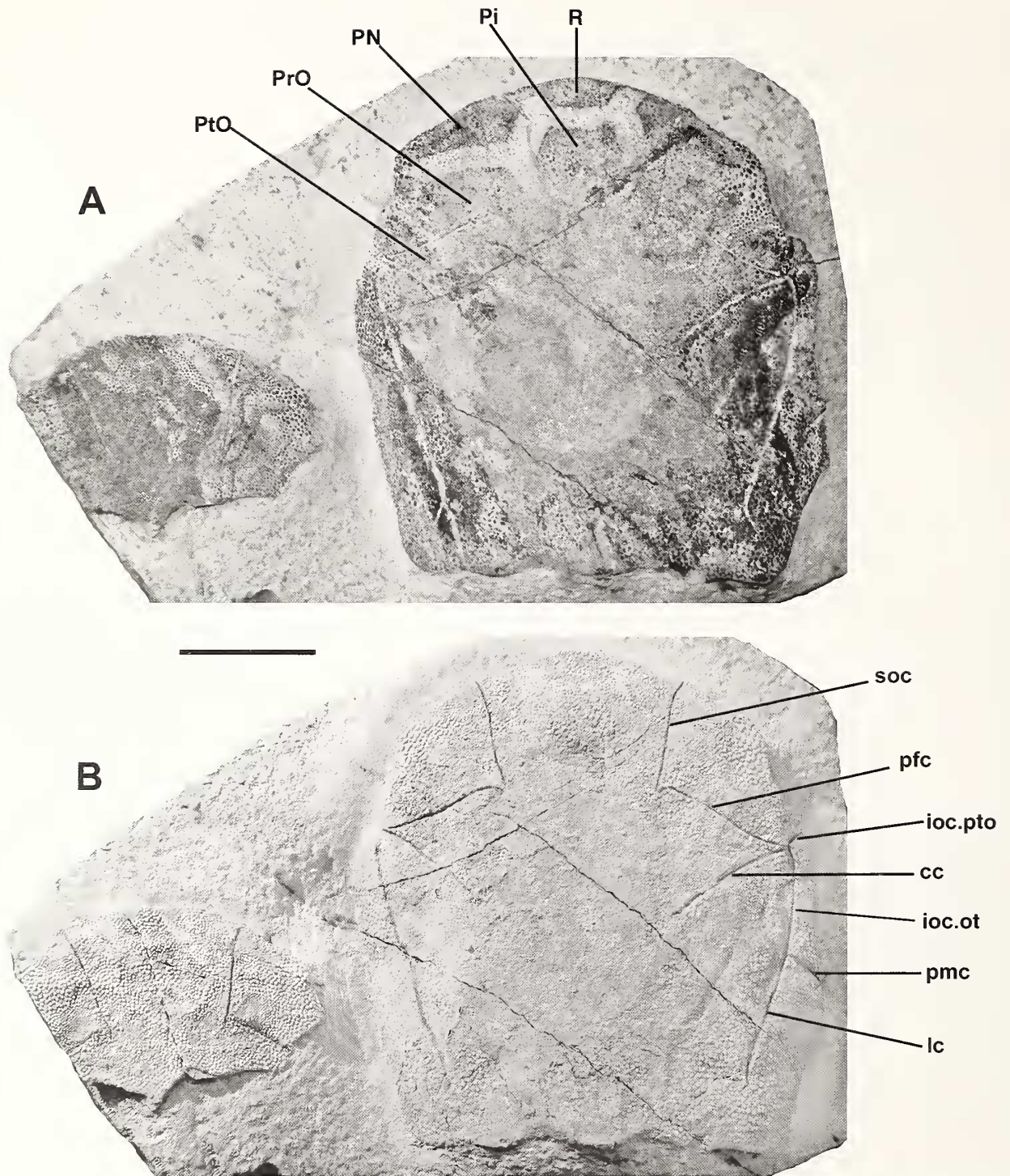
Figure 3. *Bryantolepis williamsi* n. sp. Holotype skull roof, KUVP 141304, and rostral area of a second skull, KUVP 141305. A, uncoated to show the plates of the anterior part of the skull; B, coated with ammonium chloride to show the sensory canals. Key as in Figure 1. Scale bar equals 1 cm.
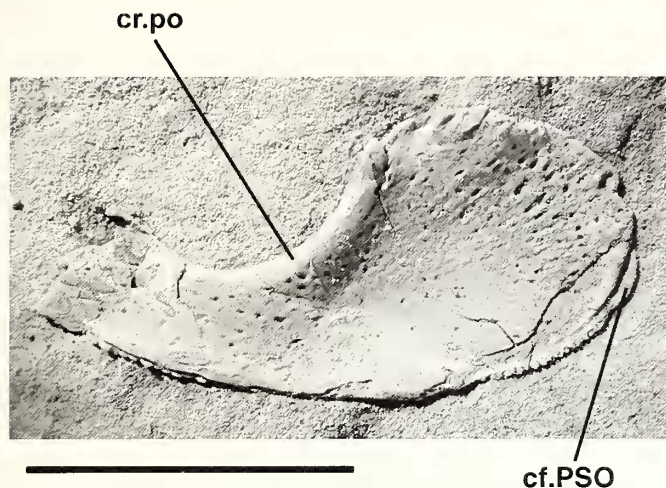
Figure 4. *Bryantolepis williamsi* n. sp. Right suborbital plate, KUVP 141307, in visceral view. Key: cr.po, postocular crista; cf.PSO, contact face for postsuborbital plate. Scale bar equals 1 cm.

Gnathal element

The left anterior superognathal is attached to the anterior part of a ridge developed on the ethmoid region of the endocranium (Figures 5–7). The posterior superognathal is unfortunately missing but would have occupied a position posterior to the anterior superognathal (supported by the autopalatine portion of the palatoquadrate). The anterior superognathal is oval, and 2.0 mm long by 1.5 mm broad. It is covered by small tubercles similar in size and shape to those present over the anterior part of the parasphenoid. Tubercles become larger and taller around the anterior and medial edges of the plate, forming a raised edge. The ossification center is indicated by a cluster of the smallest tubercles. Greatest amount of growth is in the direction of the larger anterior and medial tubercles. The occlusal surface of the element is not parallel to the endocranial surface but slopes steeply dorso-medially, thus there is a thickened face anterolaterally. A few tubercles are found on this vertical face.

The superognathals are poorly known in actinolepidoids. Denison (1958) described from the Water Canyon Formation a broad elongated plate with a smooth occlusal surface and with a group of tubercles on one side. He identified this as a posterior superognathal and noted that it may have belonged to an actinolepidoid although he was not able to positively identify it. He also described an additional and smaller plate that was also smooth on its occlusal surface and that may have been an anterior superognathal (Miles, 1969). Denison (1960) identified a small gnathal plate of uncertain position from the Holland Quarry Shale where it occurs with *Proaethaspis ohioensis* (Denison, 1960). It is a broad element with a few blunt ridges and worn teeth, identified as a crushing dentition (Denison, 1960). Stensiö (1963b) described an anterior superognathal in place in a specimen of *Kujdanowiaspis* as a "comparatively high but rostro-caudally fairly thin bone" oriented transversely in the skull and with a series of small ventral tubercles along its edge. However, the condition described by Stensiö is a byproduct of weathering (D. Goujet, personal communication, 2010). Dupret (2010, p. 30) describes the anterior superognathal as a wider than long flat structure with tubercles confined to the anterior portion that he equates with a non-shearing primitive character state. This
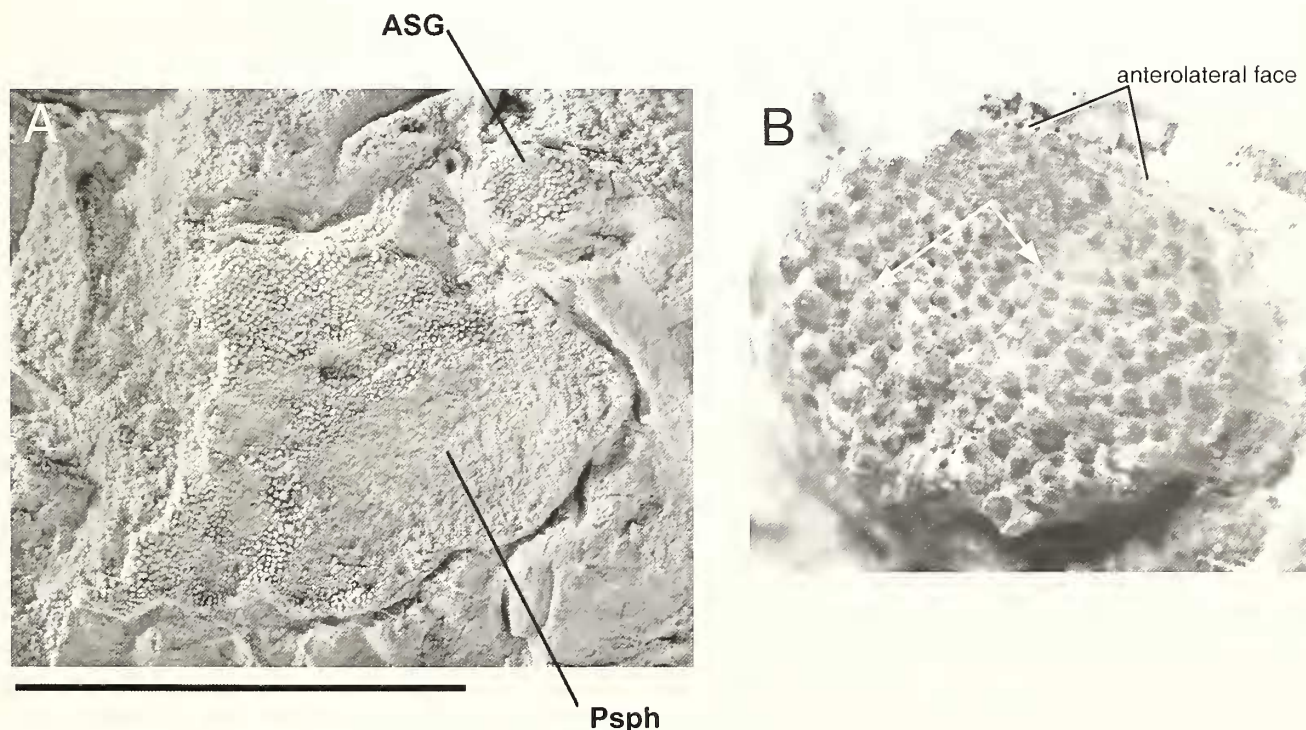

Figure 5. *Bryantolepis williamsi* n. sp. A, detail of endocranium KUVP 141308 to show the parasphenoid and anterior superognathal; B, close-up of the anterior superognathal. Arrows indicate the direction of growth from the ossification center. Additional tubercles are located on the anterolateral face. Key: ASG, anterior superognathal; Psph, parasphenoid. A, scale bar equals 5 mm.
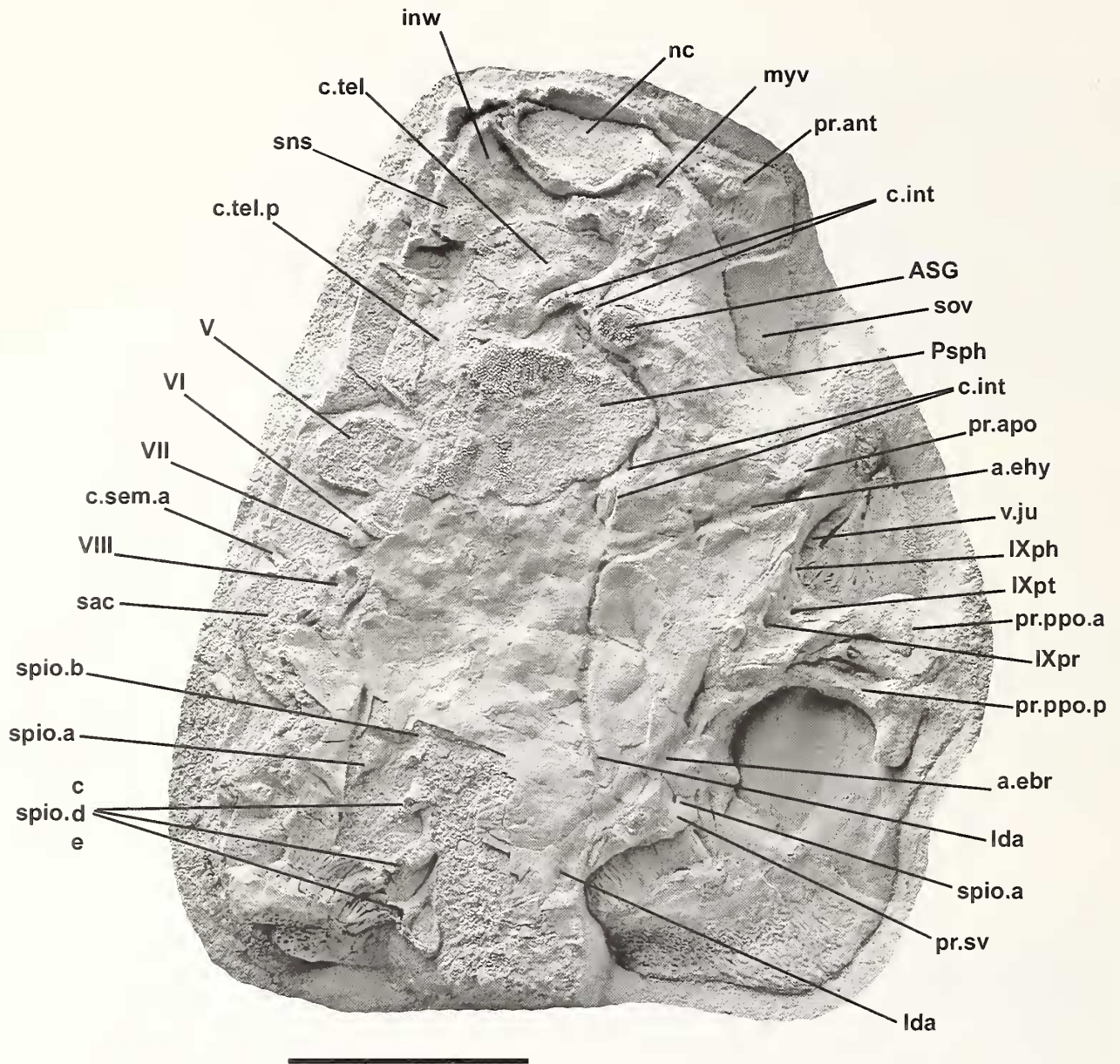
Figure 6. *Bryantolepis williamsi* n. sp. Endocranium KUVP 141308 in ventral view. Key: a.ehy, efferent hyoid artery; a.ebr, efferent branchial artery; ASG, anterior superognathal; c.int, internal carotid; c.sem.a, anterior semicircular canal; c.tel., cavity for the telencephalon; c.tel.p, cavity for posterior part of the telencephalon; inw, internasal wall; lda, lateral dorsal aorta; myv, ventral myodome of the orbit; nc, nasal capsule; pr.ant, antorbital process; pr.apo, anterior postorbital process; pr.ppo.a, anterior branch of the posterior postorbital process; pr.ppo.p, posterior branch of the posterior postorbital process; pr.sv, supravagal process; Psph, parasphenoid; sac, sacculus; sns, subnasal shelf; sov, supraorbital vault; spio.a–e, spino-occipital nerves; V, maxillary and mandibular branches of trigeminal nerve; VI, abducens nerve; VII, facial nerve; VIII, acoustic nerve; v.ju, canal for jugular vein; IXph, glossopharyngeal nerve, pharyngeal branch; IXpr, glossopharyngeal nerve, pretrematic branch; IXpt, glossopharyngeal nerve, posttrematic branch. Scale bar equals 1 cm.

appears to be the condition described here from *Bryantolepis*, although the entire plate surface is tuberculated.

The anterior superognathal of *Bryantolepis* is only the second for an actinolepidoid that is positively identified due to being attached to a skull. In contrast with that seen in more advanced forms such as *Coccosteus*, which is a shearing plate, the plate in *Bryantolepis* is clearly adapted for crushing and indicates an early development of this specialization.

Endocranium

Specimen KUVP 141308 is a skull roof exposed in ventral view and preserving the endocranium (Figure 6). Much of the right side and part of the anterior was removed by weathering prior to collection and the perichondral laminae lining the cavities and canals within the endocranium were exposed in that area. Preparation has further exposed these structures and the ventral surface of the left side of the endocranium allowing identification
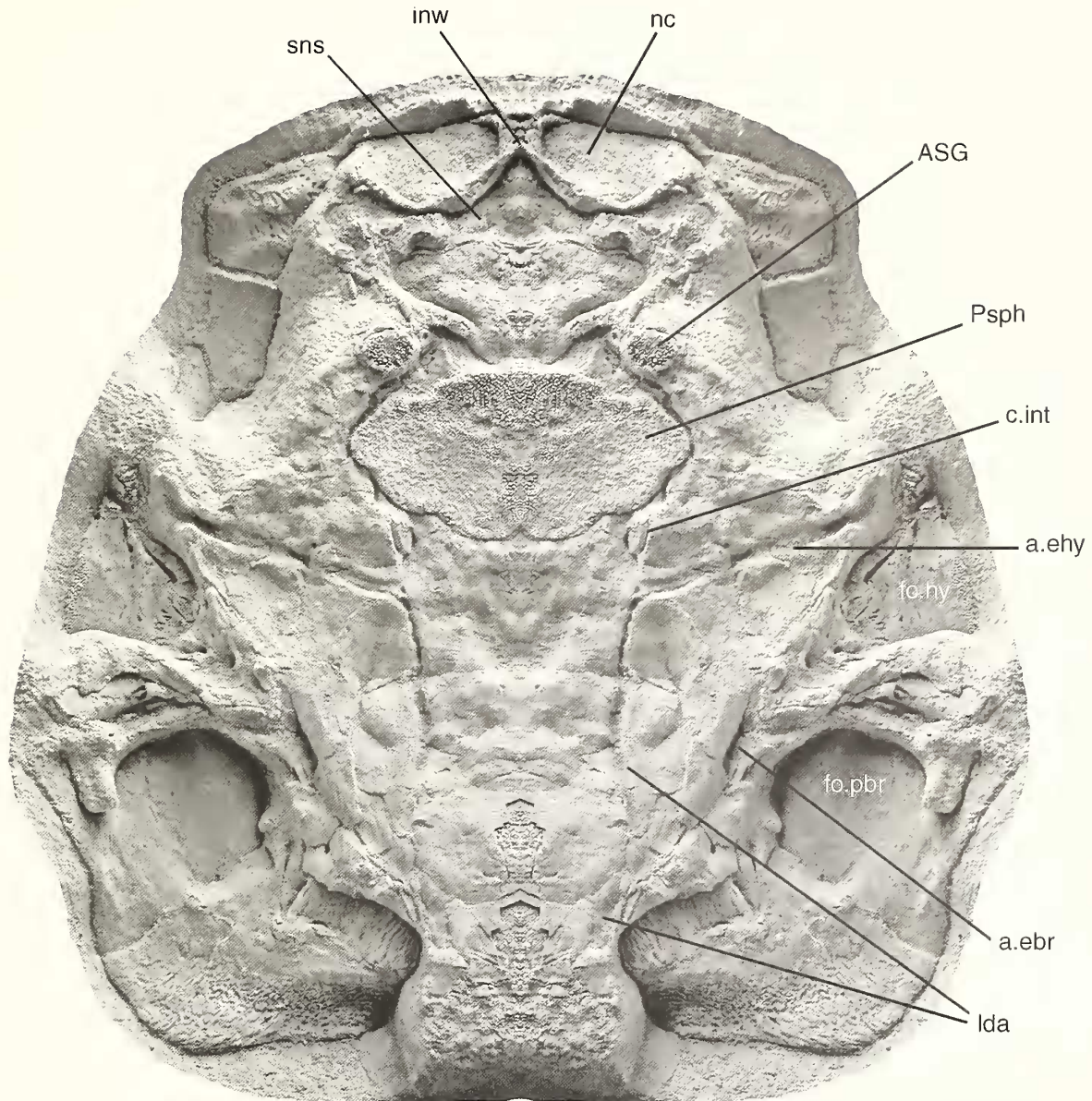
Figure 7. *Bryantolepis williamsi* n. sp. Reconstruction of the endocranium in ventral view, made by mirror-imaging the left side of the specimen as preserved. Key, as for Figure 6, plus fo.hy, hyoid muscle fossa; fo.pbr, parabranchial fossa. Scale bar equals 1 cm.

of the major features. Although generally well-preserved, the bone forming the ventral surface of the endocranium is very thin and has been crushed or distorted in some areas. An overall reconstruction has been attempted by mirror-imaging the more complete left side (Figure 7). Identification of the major features is based on the reconstructions of the endocranial cavities and canals in *Kujdanowiaspis* (Stensiö, 1963b; Dupret, 2010), and *Lehmanosteus* (Goujet, 1984) as these are the only other actinolepidoids for which such information is available. Additional information has been taken from the work of Young (1979, 1981) on *Buchanosteus* Stensiö, 1945, and *Errolosteus* Young, 1981.

The lateral wall of the endocranium is fused to the ventral surface of the dermal skull roof and forms a series of processes

and embayments. The interpretation of homology for these processes and fossae and the subsequent nomenclature applied has varied (contrast Young, 1980, with Goujet, 1984, and Dupret, 2010). Interpretations by Goujet and Young (Figure 8) have differed in their interpretation of bounding foramina, differing in their identification of the foramen in the posterior part of the anterior parajugular fossa (pr.pja) in *Macropetalichthys*. Goujet (personal communication, 2010) interprets this as the glossopharyngeal foramen (IX, Figure 8B) while Young places this foramen in the posterior parajugular fossa (fo.pjp, Figure 8A). While using similar defining characteristics for the processes, it is the difference in cranial nerve sequence that leads to alternative process identifications. Although beyond the scope of the current study, resolution of these questions is important for resolving the
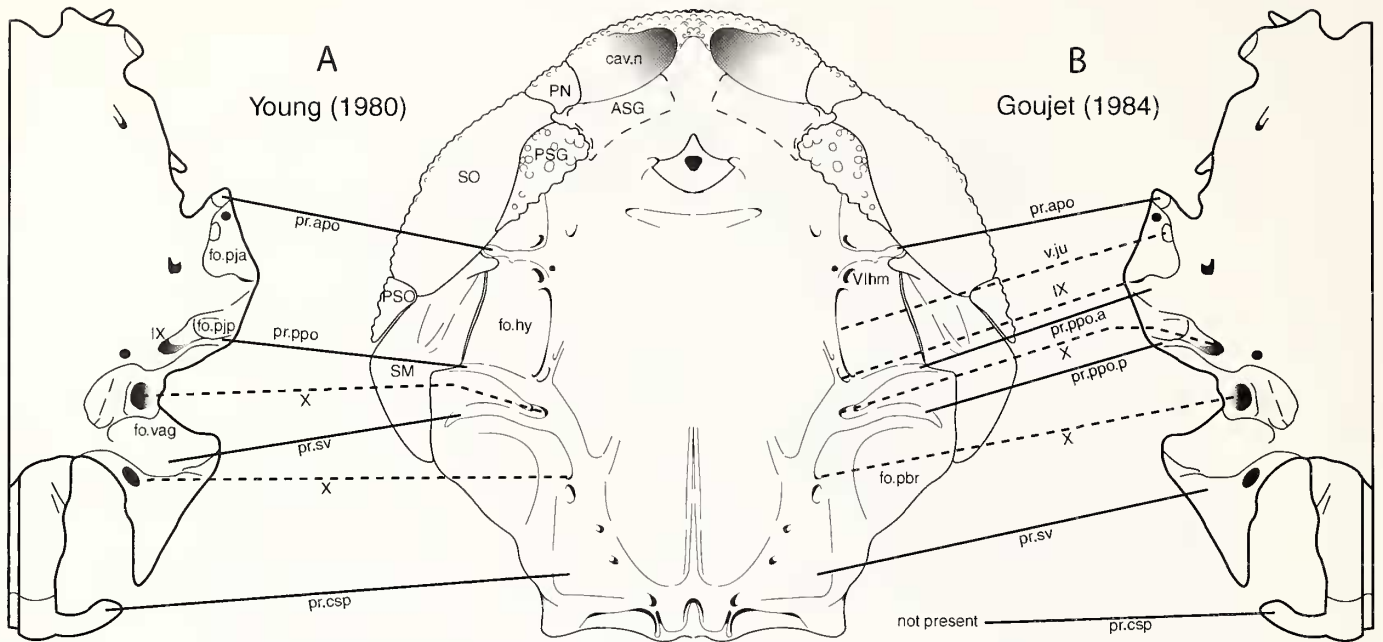
Figure 8. Proposed homologies of the processes and fossae between *Dicksonosteus* (center; after Goujet, 1984) and *Macropetalichthys* (right and left; after Young, 1980). A, interpretation after Young (1980). B, interpretation after Goujet (1984). Solid lines for processes, dashed lines for foramina. Key: as for Figure 6, plus fo.pja, anterior parajugular fossa; fo.pjp, posterior parajugular fossa; fo.vag, vagus fossa; PN, postnasal plate; pr.csp, craniospinal process; pr.ppo, posterior postorbital process; PSG, posterior superognathal plate; PSO, postsuborbital plate; SM, submarginal plate; SO, suborbital plate; VIIhm, hyomandibular branch of the facial nerve foramen.

content and function for the processes and bounded fossae (visceral arch attachments, muscle insertions, and branchial and parabranchial chambers). Nomenclature in this study follows that of Goujet (1984) and Dupret (2010) (both interpretations are presented, without favor, to permit comparison of the condition in *Bryantolepis williamsi* n. sp. to other described taxa). An interpretive reconstruction of the endocranial cavities and canals is provided (Figure 9). Posteriorly the supravagal process (pr.sv, Figures 6, 9) has been somewhat crushed and little detail can be seen. Its posterior limits can be discerned on the right side. The surface of the endocranium and the skull roof in this area is roughened and pitted presumably for muscle attachment. Anterior to this a broad parabranchial fossa (sensu Carr et al., 2009; cucullaris fossa sensu Goujet, 1984) is recessed into the endocranial wall and is delimited anteriorly by the posterior postorbital process, which forms a conspicuous lateral feature. This process is bifid (pr.ppo.a, pr.ppo.p) as in the actinolepidoids *Kujdanowiaspis* (Stensiö, 1963b, fig. 41) and *Lehmanosteus* (Goujet, 1984, fig. 107), but unlike the brachythoracid *Buchanosteus* (Young, 1979, fig. 2), which has a single process only. Young (1979, p. 315–316) has suggested that the anterior branch of this process is homologous to the postorbital process in *Buchanosteus* and that the posterior branch is homologous to the supravagal process in *Macropetalichthys* Norwood and Owen, 1846 (Stensiö, 1969, fig. 22A). Based on this he concludes that the fossa enclosed by the branches is homologous to the paravagal fossa of *Macropetalichthys* (Figure 8A), that it contained muscles controlling the operculum, and that its presence may be associated with the presence of a large submarginal plate, considered to be a primitive feature. Although the submarginal plate is not known in *Bryantolepis williamsi* n. sp. it is reconstructed as a large plate in

the only other species *B. brachycephala* (Denison, 1962, fig. 57; Denison, 1978, fig. 34; apparently based on a composite reconstruction using cheek plates identified as "Arctolepida indet.," Denison, 1958, fig. 103C, D). The presence of an internal groove, suggestive of a groove for the epihyal, implies that the submarginal as reconstructed by Denison, 1978, fig. 34, is antero-posteriorly reversed. Following Young (1980), the reduced vagal fossa (fo.vag, Figure 8) in *Bryantolepis williamsi* n. sp. implies a reduced musculature for a relatively large operculum.

Between the posterior (pr.ppo) and anterior (pr.apo) postorbital processes is a short hyoid muscle fossa (fo.hy, Figure 8). The lateral wall of this fossa contains foramina for the pharyngeal, pre-, and posttrematic branches of the glossopharyngeal nerve (IXph, IXpt, IXpr, Figures 6, 9). A foramen and short groove in this area probably represents the position of the canal that bore the jugular vein (v.ju, Figure 6). Anterior to the anterior postorbital process the endocranium is crushed and the mandibular fossa cannot be recognized, however, there is a deep orbital cavity roofed by the dermal bone of the skull roof.

The ventral surface of the endocranium is marked by a series of branching grooves, best seen on the left side (Figures 6, 7). These represent the position of the two lateral vessels of the dorsal aorta (lda) and its branches, which proceed anteriorly. That on the left can be followed to the level of the supravagal process at which point the lateral aorta continues anteriorly while the efferent branchial artery (a.ebr) branches off laterally and runs parallel to the margin of the parabranchial fossa (fo.pbr). The anterior portion of the lateral dorsal aorta divides again at the level of the hyoid muscle fossa. At this point the efferent hyoid artery (a.ehy) branches laterally and continues along the ventral surface of the anterior postorbital process, while the internal carotid artery
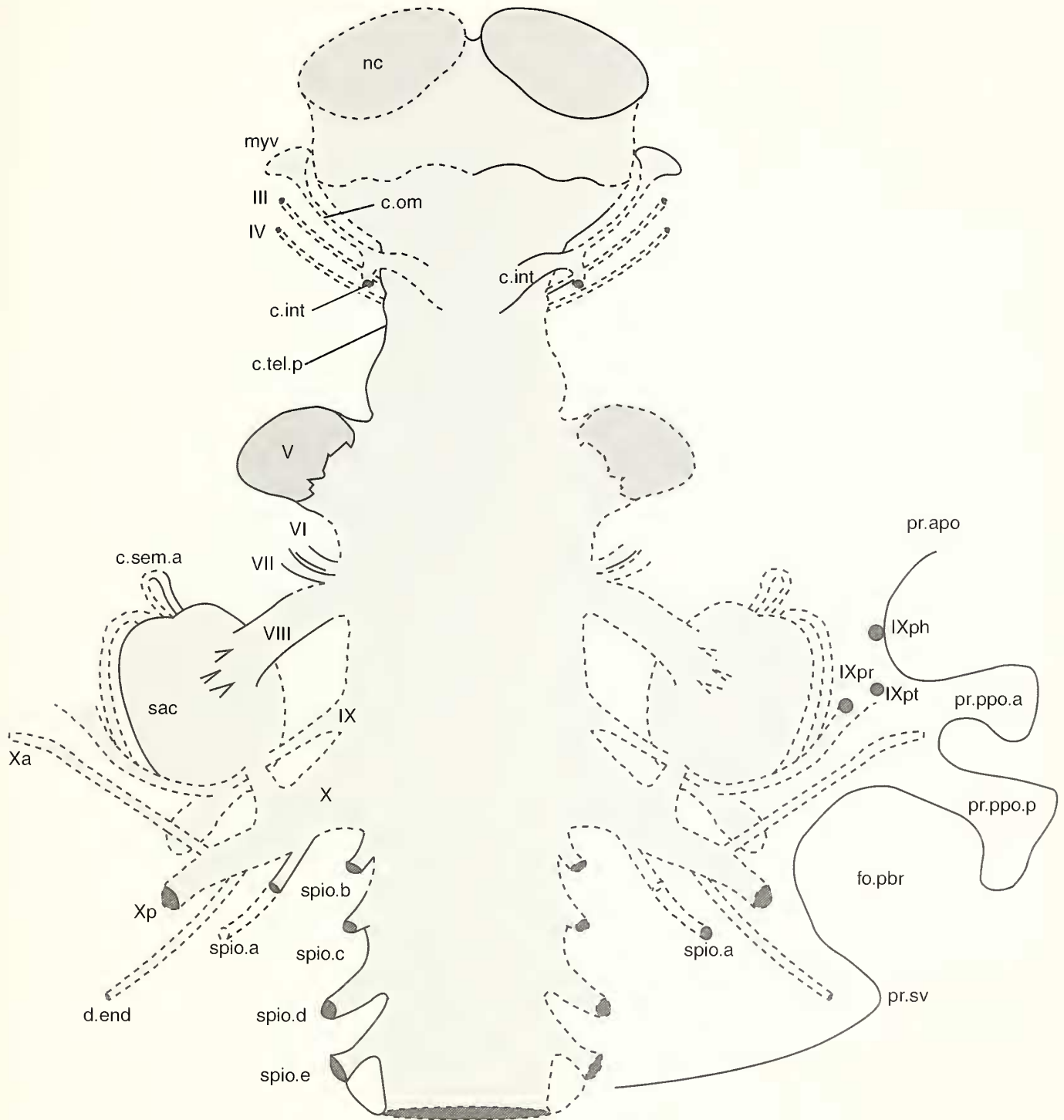
Figure 9. Proposed reconstruction of the cranial endocast in *Bryantolepis williamsi* n. sp. Based on the endocranium in KUVP 141308 (Figure 6). Solid lines represent preserved structures. Dashed lines represent hypothesized features. Reconstruction of hypothetical features are based on *Kujdanowiaspis* (Goujet, 1984, fig. 29). Known structures, limited to the right or left, are reconstructed on the opposite side as mirror-images. The posterolateral outline of the neurocranium is shown for the left side to provide a reference for known foramina. The posterior extent of the supravagal process is based on its fragmented presence on the right side and on impressions of the process on the internal face of the dermal skull roof. Key: as for Figure 6, plus III, occulomotor nerve; IV, trochlear nerve; c.om, canal for the opthalmica-magna artery; Xa, anterior branch of the vagus nerve; Xp, posterior branch of the vagus nerve; d.end, endolymphatic duct.

(c.int) runs anteriorly before entering a foramen and running a short distance in a canal which vanishes dorsal to the lateral margin of the parasphenoid (Psph). In *Lehmanosteus* (Goujet, 1984, fig. 107) and *Kujdanowiaspis* (Stensiö, 1963b, fig. 14) the internal carotid apparently continued in a groove lateral to the parasphenoid, however, the parasphenoid in *Bryantolepis williamsi* n. sp. is a large plate leaving no lateral space for this to happen.

Other structures on the ventral surface of the endocranium include the previously described parasphenoid and left anterior superognathal (Figure 6, Psph, ASG) and anterior to them the left nasal capsule (nc). Although partly removed by weathering it shows an oval cavity walled by the dermal rostral bone anteriorly but posteriorly by a thin wall of perichondral bone. Medially part of the internasal wall is preserved (inw). This rises medially suggesting the presence of a median ridge (Figure 7) and where exposed laterally by weathering it is seen to lie ventral to the dermal rostral bone. Posterior to the nasal capsule the subnasal shelf (sns) appears to meet the ossification surrounding the telencephalon (c.tel) along a sinuous margin. The connection between this and the nasal capsule is through the olfactory tract and bulb, neither of which is visible here. A crushed area posterolateral to the nasal capsule and triangular in shape may represent the position of the ventral myodome in the orbit (myv, Figures 6, 9). On the posterolateral surface of the telencephalon and anterior to the parasphenoid a canal rises and continues anterolaterally. This is the canal for the internal carotid artery (c.int), which subsequently divides in *Kujdanowiaspis* (Stensiö, 1963b; fig. 30) to form the canal for the opthalmica-magna artery (Young, 1979, p. 329; c.om, Figure 9), which then leads into the ventral myodome. Unfortunately this area has been crushed and weathered so that the canal cannot be traced into the myodome, however, a small foramen just anteromedial to the anterior superognathal leading into a canal that lies medial to the superognathal may be the branch of the internal carotid that connects posteriorly, dorsal to the lateral margin of the parasphenoid.

The right side of the endocranium was weathered obliquely, almost to the midline anteriorly, and a little less posteriorly, exposing the perichondral laminae lining the cavities and canals within the endocranium (Figures 6, 9). Posteriorly five canals in series can be seen projecting from within the endocranium and these appear to be canals surrounding five spino-occipital nerves (spio.a–e). The foramina for these nerves should be visible in the surface of the supravagal process on the left side but crushing and loss has obscured all but one (spio.a). The canal for the anterior spino-occipital nerve on the right side is in close-proximity to the vagal recess (not preserved). This position could imply that the anterior spino-occipital nerve may be associated with the vagus nerve, possibly a posterior lateral-line nerve. On the left side the foramina for the pretrematic and posttrematic branches of the glossopharyngeal nerve can be seen on the anterior surface of the base of the posterior postorbital process (IXpr, IXpt). The foramen for the pharyngeal branch is present in the lateral wall of the hyoid muscle fossa (IXph). At the level of the posterior postorbital process, on the right side, a part of the labyrinth cavities is preserved. This is an oval structure that represents the cavity for the sacculus (sac). The external semicircular canal has been eroded but a short section of canal that leads anterolaterally from the sacculus probably represents part of the anterior semicircular canal (c.sem.a), which would then continue dorsally. The canal for the acoustic nerve (VIII, Figures 6, 9) is visible and

has a branching connection to the sacculus. None of the ampullae have been preserved.

The canals for the facial and abducens nerves (VII, VI, Figures 6, 9) can be traced just anterior to that for the acoustic nerve. Anterior to these and lateral to the posterior part of the parasphenoid is a large canal preserved at its branch from the cranial cavity which from its position is most likely to be the canal for the maxillary and mandibular branches of the trigeminal nerve (V). The canal for the pituitary vein is a large ossified structure in *Buchanosteus* (Young, 1979, fig. 6) but appears to be much smaller in actinolepidoids such as *Kujdanowiaspis* (Stensiö, 1963b, fig. 30) where it is not carried in an ossified canal. Canals for the oculomotor (III) and trochlear (IV) nerves should be present at the level of the anterior part of the parasphenoid but cannot be seen here (reconstructed in Figure 9). In this region the lateral portion of the posterior part of the telencephalon (c.tel.p) can be seen.

The endocranium of actinolepidoids is well known from the work of Stensiö (1963b) in which specimens of *Kujdanowiaspis* were serially sectioned to provide an immense amount of information on the shape of the cranial cavity and the position of canals and foramina for the cranial nerves and vessels. The only additional information on the cranial anatomy of an actinolepidoid comes from specimens of *Lehmanosteus* (Goujet, 1984, fig. 107) in which the ventral surface of the endocranium was preserved. The endocranium of *Bryantolepis williamsi* n. sp. is in accord with the information known for the other actinolepidoids, differing only in the greater clarity of the grooves and canals for blood vessels on the ventral surface of the endocranium, which allows a more complete picture of their distribution to be seen and shows that the internal carotid is present in a canal dorsal to the lateral margin of the parasphenoid in this species.

Trunk shield

The only trunk shield material (KUVP 141306) consists of a single specimen found in association with the type skull and comprising the right anterior ventrolateral, anterior-ventral, interolateral, and spinal plates (Figure 10). These are essentially as in the described species *B. brachycephala* (Denison, 1958, fig. 112G) with the only important difference being that the new specimen is almost twice as large.

Actinolepidoid Relationships

The order Arthrodira has been divided into two main complexes, the "dolichothoracids" with a long trunk armor and the "brachythoracids" with a short armor (Stensiö, 1944). The dolichothoracids are now considered not to be a natural group but one that represents an evolutionary grade (Goujet, 1984) and that consists of two subgroups, the Actinolepidoidei Miles, 1973, and the Phlyctaenii Miles, 1973. The actinolepidoids have been considered a clade by some workers (Long, 1984, his Actinolepidi + Wuttagoonaspidi + Phyllolepidi), and this was assumed by Johnson et al. (2000) in their first cladistic analysis of the group. Although they selected the Petalichthyida as the outgroup they had only the actinolepidoids as the ingroup making it impossible to test actinolepidoid monophyly (Dupret, 2004). Analyses by Dupret and Dupret and others incorporated characters from a new description of *Kujdanowiaspis* (Dupret, 2004) and a basal member of the Actinolepidoidei (Dupret et al., 2009), as well as the best-known actinolepidoids together with phlyctaeniids and brachythoracids. These analyses showed that the "Actinolepidoi-
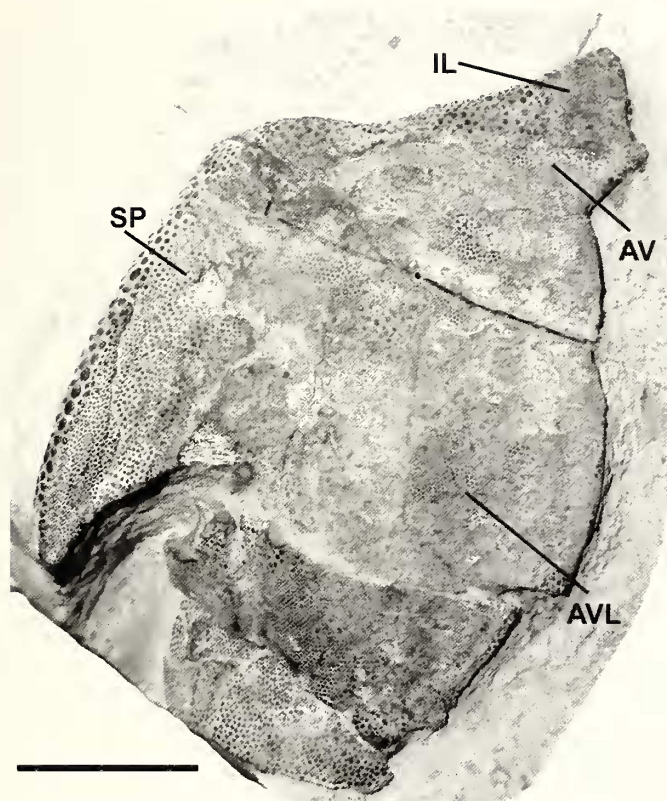
Figure 10. *Bryantolepis williamsi* n. sp. Right anterior part of ventral armor, KUVP 141306. Key: AV, anterior-ventral plate; AVL, anterior ventrolateral plate; IL, interolateral plate; SP, spinal plate. Scale bar equals 1 cm.

dei" is a paraphyletic group (with or without *Wuttagoonaspis* and/ or the phyllolepids) and that the Wuttagoonaspididae and the paraphyletic antarctaspids represent the basal-most members of the Arthrodira (Dupret, 2009, fig. 3; Figure 1).

Bryantolepis brachycephala, the previously only known species, is shown in the latter analysis to be an isolated taxon forming a sister group to the Phlyctaenioidei (Dupret, 2009, fig. 3; Figure 1). The new species of *Bryantolepis* described here adds nothing to knowledge of the external morphology of the genus, however; Dupret (2004) developed four characters for the endocranium that could not be scored for *Bryantolepis* at the time of the analysis but can be assessed now.

Character 1 is "Connection between endocranial ethmoid and postethmoid components. 0: no connection; 1: connection produced by osseous trabecules or fusion." It is noted (Dupret, 2004) that no connection is observed in all major groups of arthrodires, and preservation is not complete enough to show what the situation is in *Bryantolepis williamsi* n. sp. (scored as ?). Character 2 is "Anterior postorbital process. 0: massive; 1: thin." The description of this character was clarified by Dupret et al. (2009) to note the position of the hyomandibular branch of the facial nerve ("0: foramen in the distal part of the anterior postorbital process" and "1: foramen in a proximal and posterior position"). It is the position of this nerve that correlates with a massive process (D. Goujet, personal communication, 2010; compare Goujet, 1984, figs. 51 and 52, *Dicksonosteus* and

Kujdanowiaspis, respectively). The new specimen is preserved in ventral view and the anterior postorbital process does appear to be massive based on its similarity in size to that of *Kujdanowiaspis* (Stensiö, 1963b, fig. 25) (scored as 0). Character 3 is "Supraorbital process. 0: absent; 1: present." This process is present only in actinolepidoids (Goujet, 1984) but is not exposed in the new specimen (scored as ?). Character 4 is "Basal process. 0: absent; 1: present." This process is again only present in actinolepidoids and can be seen in the new specimen (scored as 1).

Adding the new scoring to the matrix of Dupret et al. (2009) for *B. brachycephala* (assuming that characters 2 and 4 of *Bryantolepis williamsi* n. sp. are consistent within the genus) and running the analysis does not result in any change to the position of *Bryantolepis* in the published tree (Dupret et al., 2009, fig. 3; Figure 1). Due to missing data for *Bryantolepis williamsi* n. sp. (characters 17, 18, 29, 30, 36, 42, 43, 46–48, 51–54, 59–62, and 64–65; most related to incomplete knowledge of the trunk shield), addition of this taxon to the analysis reduces the resolution of tree topology only in the case of *Bryantolepis* (individual species form a polytomy with the Phlyctaenioidei, Actinolepididae, and node "**" of Figure 1 [node 8 of Dupret et al., 2009, fig. 3]).

References

Agassiz, L. J. R. 1839. Fishes of the Old Red Sandstone, p. 589–602. *In* R. I. Murchison, The Silurian System, Part II. John Murray, London.

Branson, E. B., and M. G. Mehl. 1931. Fishes of the Jefferson Formation of Utah. Journal of Geology, 39:509–531.

Bryant, W. L. 1932. Lower Devonian fishes of Bear Tooth Butte, Wyoming. Proceedings of the American Philosophical Society, 71:225–254.

Bryant, W. L. 1934. The fish fauna of Beartooth Butte, Wyoming: Parts II and III. Proceedings of the American Philosophical Society, 73:127–162.

Bryant, W. L. 1935. *Cryptaspis* and other Lower Devonian fossil fishes from Beartooth Butte, Wyoming. Proceedings of the American Philosophical Society, 75:111–128.

Camp, C. L., S. P. Welles, and M. Green. 1949. Bibliography of fossil vertebrates, 1939–1943. Geological Society of America Memoir 37. 371 p.

Carr, R. K., Z. Johanson, and A. Ritchie. 2009. The phyllolepid placoderm *Cowralepis mclachlani*: insights into the evolution of feeding mechanisms in jawed vertebrates. Journal of Morphology, 270:775–804.

Davis, R. L. 1983. Geology of the Dog Valley-Red Ridge area, southwest Pavant Mountains, Millard County, Utah. Brigham Young University Geology Studies, 30:19–36.

Dehler, C. M. 1995. Paleoenvironmental and stratigraphic analysis of Lower Devonian Beartooth Butte Formation and associated strata, central-eastern Idaho. Unpublished master's thesis, Northern Arizona University, Flagstaff. 157 p.

Denison, R. H. 1953. Early Devonian fishes from Utah. Part II. Heterostraci. Fieldiana: Geology, 11:199–355.

Denison, R. H. 1958. Early Devonian fishes from Utah, Part III, Arthrodira. Fieldiana: Geology, 11:461–551.

Denison, R. H. 1960. Fishes of the Devonian Holland Quarry Shale of Ohio. Fieldiana: Geology, 11:555–613.

Denison, R. H. 1962. A reconstruction of the shield of the arthrodire, *Bryantolepis brachycephalus* (Bryant). Fieldiana: Geology, 14:99–104.

Denison, R. H. 1968. Early Devonian lungfishes from Wyoming, Utah, and Idaho. Fieldiana: Geology, 17:353–413.

Denison, R. H. 1978. Handbook of Paleoichthyology 2, Placodermi. H-P. Schultze (ed.), Gustav Fischer Verlag, Stuttgart. 128 p.

Dennis-Bryan, K. 1995. Some comments on the placoderm parasphenoid. Bulletin du Muséum National d'Histoire Naturelle, 17:127–142.

Dupret, V. 2004. The phylogenetic relationships between actinolepids (Placodermi: Arthrodira) and other arthrodires (phlyctaeniids and brachythoracids). Fossils and Strata, 50:44–55.

Dupret, V. 2010. Revision of the genus *Kujdanowiapis* Stensiö, 1942 (Placodermi, Arthrodira, "Actinolepida") from the Lower Devonian of Podolia (Ukraine). Geodiversitas, 32:5–63.

Dupret, V., Z. Min, and J.-Q. Wang. 2009. The morphology of *Yujiangolepis liujingeusis* (Placodermi, Arthrodira) from the Pragian of Guangxi (south China) and its phylogenetic significance. Zoological Journal of the Linnean Society, 157:70–82.

Eichwald, C. E. von. 1840. Die Their- und Pflanzenreste des alten rothen Sandsteins und Bergkalks im Novgorodschen Gouvernement. Bulletin de l'Académie Impériale des Sciences de Saint Pétersbourg, 7:78–91.

Elliott, D. K., and R. R. Ilyes. 1996. New Early Devonian pteraspidids (Agnatha, Heterostraci) from Death Valley National Monument, southeastern California. Journal of Paleontology, 70:152–161.

Elliott, D. K., and H. G. Johnson. 1997. Use of vertebrates to solve biostratigraphic problems: examples from the Lower and Middle Devonian of Western North America, p. 179–188. *In* G. Klapper, M. A. Murphy, and J. A. Talent (eds.), Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography: Studies in Honor of J. Granville ("Jess") Johnson. Geological Society of America Special Paper 321.

Elliott, D. K., H. G. Johnson, R. Cloutier, R. K. Carr, and E. B. Daeschler. 2000. Middle and Late Devonian vertebrates of the western Old Red Sandstone Continent, p. 291–308. *In* A. Blieck and S. Turner (eds.), Palaeozoic Vertebrate Biochronology and Global Marine/Non-Marine Correlation. Frankfurt am Main, Courier Forschungsinstitut Senckenberg, 223.

Gardiner, B. G., and R. S. Miles. 1990. A new genus of eubrachythoracid arthrodire from Gogo, western Australia. Zoological Journal of the Linnean Society of London, 99:159–204.

Goujet, D. 1984. Les poissons placodermes du Spitsberg: Arthrodires Dolichothoraci de la Formation de Wood Bay (Dévonien inférieur). Cahiers de Paléontologie, CNRS. 284 p.

Johnson, H. G., D. K. Elliott, and J. H. Wittke. 2000. A new actinolepid arthrodire (Class Placodermi) from the Lower Devonian Sevy Dolomite, east-central Nevada. Zoological Journal of the Linnean Society of London, 129:241–266.

Johnson, J. G., G. Klapper, and C. A. Sandberg. 1985. Devonian eustatic fluctuations in Euramerica. Geological Society of America Bulletin, 96:567–587.

Johnson, J. G., and C. A. Sandberg. 1977. Lower and Middle Devonian continental-shelf rocks of the western United States, p. 121–143, *In* M. A. Murphy, W. B. N. Berry, and C. A. Sandberg (eds.), Western North America: Devonian. University of California, Riverside Campus Museum Contribution 4.

Johnson, J. G., C. A. Sandberg, and F. G. Poole. 1988. Early and Middle Devonian paleogeography of western United States, p. 161–182. *In* N. J. McMillan, A. F. Embry, and D. G. Glass (eds.), Devonian of the World. Canadian Society of Petroleum Geologists Memoir 14.

Long, J. A. 1984. New phyllolepids from Victoria and the relationships of the group. Proceedings of the Linnean Society of New South Wales, 107:263–308.

M'Coy, F. 1848. On some new fossil fish of the Carboniferous period. Annals and Magazine of Natural History, 2:1–10, 115–133.

Miles, R. S. 1969. Features of placoderm diversification and the evolution of the arthrodire feeding mechanism. Transactions of the Royal Society of Edinburgh, 68:123–170.

Miles, R. S. 1973. An actinolepid arthrodire from the Lower Devonian Peel Sound Formation, Prince of Wales Island. Palaeontographica, Abteilung A, 143:109–118.

Norwood, J. G., and D. D. Owen. 1846. Description of a new fossil fish from the Palaeozoic rocks of Indiana. American Journal of Science, 2:367–371.

Ørvig, T. 1961. Notes on some early representatives of the Drepanaspida (Pteraspidomorphi, Heterostraci). Arkiv för Zoologi, 2:515–535.

Reed, R. C. 1997. Stratigraphy and sedimentology of the Lower and Middle Devonian Water Canyon Formation, northern Utah. Unpublished master's thesis, Northern Arizona University, Flagstaff. 322 p.

Stensiö, E. A. 1942. On the head of certain Arthrodires. Kungliga Svenska Vetenskapsakademiens Handlingar, 20:1–32.

Stensiö, E. A. 1944. Contributions to the knowledge of the vertebrate fauna of the Silurian and Devonian of Podolia II: notes on two arthrodires from the Downtonian of Podolia. Arkiv för Zoologi, 35A(9):1–83.

Stensiö, E. A. 1945. On the head of certain arthrodires. II. On the cranium and cervical joint of the Dolichothoraci (Acanthaspida). Kungliga Svenska Vetenskapsakademiens Handlingar, 22:1–70.

Stensiö, E. A. 1963a. The brain and cranial nerves in fossil, lower craniate vertebrates. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Matematisk-naturvidenskapelig klasse. New Series, 13:1–20.

Stensiö, E. A. 1963b. Anatomical studies on the arthrodiran head. Part I. Preface, geological and geographical distribution, the organization of the head in the Dolichothoraci, Coccosteomorphi and Pachyosteomorphi. Taxonomic appendix. Kungliga Svenska Ventenskapsakademiens Handlingar, (4)9:1–419.

Stensiö, E. A. 1969. Elasmobranchiomorphi Placodermata Arthrodires, p. 71–692. *In* J. Piveteau (ed.), Traité de Paléontologie, 4(2). Masson, Paris.

Stokes, W. L. 1986. Geology of Utah. Utah Museum of Natural History and Utah Geological and Mineral Survey, Salt Lake City. 280 p.

Swofford, D. L. 2002. PAUP* Phylogenetic Analysis Using Parsimony (*and other methods), Version 4. Sinauer Associates, Sunerland.

Tanner, W. 1983. A fossil flora from the Beartooth Butte Formation of northern Wyoming. Unpublished Ph.D. thesis, Southern Illinois University, Carbondale. 208 p.

Williams, J. S., and M. E. Taylor. 1964. The Lower Devonian Water Canyon Formation of northern Utah. Contributions to Geology of the University of Wyoming, 3: 38–53.

Woodward, A. S. 1891. Catalogue of the fossil fishes in the British Museum (Natural History), 2. British Museum (Natural History), London. 567 p.

Young, G. C. 1979. New information on the structure and relationship of *Buchanosteus* (Placodermi: Euarthrodira) from the Early Devonian of New South Wales. Zoological Journal of the Linnean Society, 66:309–352.

Young, G. C. 1980. A new Early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. Palaeontographica. Abteilung A, Paläozoologie, Stratigraphie, 167:10–76.

Young, G. C. 1981. New early Devonian brachythoracids (placoderm fishes) from the Taemas-Wee Jasper region of New South Wales. Alcheringa, 5:245–271.